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# The biology of the Batbug Stricticimex antennatus (Hemiptera: Cimicidae) in South Africa

by

**W. L. Overal and L. R. Wingate**

(Departments of Entomology and Zoology, University of Natal, Pietermaritzburg)

## SYNOPSIS

A colony of *Stricticimex antennatus* Ferris & Usinger from a bat-roost near Pietermaritzburg, Natal, was estimated to contain more than 50 000 individuals. The batbugs were observed to feed on *Myotis tricolor*, *Rhinolophus simulator*, *R. clivosus*, *Nycteris thebacia*, and *Hipposideros caffer*. People entering the bat-roost were bitten, and several developed skin sensitivity to the bites. In the laboratory batbugs were fed on rabbits and rats, and found to undergo five nymphal instars. Moulting did not take place in unfed individuals. The aggregating and orientation behaviour of the batbugs in response to simple stimuli is described.

## INTRODUCTION

Since its description from specimens collected in the Cape Province from De Hoop Vlei near Bredasdorp (Ferris & Usinger 1957), *Stricticimex antennatus* has been reported from caves at Three Sisters' Rocks, Cape Province, and from a small cave in Zambia (Usinger 1966). The discovery of this species by L. R. Wingate in the course of his studies on Natal bats provided an opportunity to investigate the biology of this poorly known ectoparasite of bats.

## HABITAT AND HOSTS

The batbugs were found in an abandoned mine adit known as Doornhoek Cave which is located about 12 km east of Pietermaritzburg, Natal. The adit is a horizontal shaft which enters the hillside above a small, eroded spoil bank on the slope overlooking the Umsinduzi River. The entrance is constricted, but the shaft for its length of 73 m is about 1,7 m high and 1 m wide. The floor is uniformly covered with bat guano, and the walls and ceiling are formed of rough rock. This shaft will be fully described by Wingate (in prep.). The batbugs of both sexes and all developmental stages clustered in cracks and fissures in the ceiling and upper portions of the walls. A thorough examination of the cave in October 1954 by Dr B. R. Stuckenberg indicated that no cimicids were present at that time.

The climate of the mine is almost invarient over short time periods. Although temperatures range from 18° to 22°C and relative humidity from 42 to 96 %, changes as great as 8 % in these factors have rarely been recorded within any single week.

The shaft is a bat-roost which is utilized throughout the year, although the species composition of the bat colony changes seasonally (Wingate, in prep.). During visits to the bat-roost in February, March, April, and May 1975, *Rhinolophus simulator*, *R. clivosus*, *Myotis tricolor*, and *Hipposideros caffer* were seen. *Nycteris thebaica* has been observed by L. R. W. during other months of the year. Observations made in dim light in the shaft showed *S. antennatus* feeding on the wings or forearms of each of these bat species. This was confirmed in the laboratory for each of these host species, except *Myotis tricolor* and *Nycteris thebaica* which were not offered. Bugs fed more readily on bats than they did on rabbits, rats or human beings, and they engorged more rapidly in semi-darkness than in the light, although light did not inhibit feeding.

Both authors were bitten repeatedly by batbugs when they were in the mine, and colleagues also reported bites which became irritating several hours after their visit to the bat-roost. The batbugs appeared clumsy in walking over hairs and were fed from shaved portions of W. L. O.'s forearm. These feeding sites became swollen and red several hours after the bugs had been allowed to engorge, although the bite was painless. The reaction became progressively more pronounced with successive weekly feedings until discontinuation after three exposures. In the extreme form, reaction to the bites included pustule formation and persistent itching. When the feedings were discontinued, adults of *Cimex lectularius*, the bedbug, were allowed to feed on the same forearm used by *S. antennatus*. No immediate response to *C. lectularius* was observed, indicating no cross-reactivity, although sensitivity to *C. lectularius* soon followed.

## LIFE HISTORY

Batbugs in the laboratory were fed on rabbits whose fur was shaved from the back or flanks and, more successfully, on caged white rats on whose tails, feet, and snout the bugs congregated. The bugs pass through five nymphal instars which can be distinguished by general body size and by the width of the head, in the manner detailed by Lee (1955) for another cimicid. The head widths across the compound eyes are given in Table 1 from measurements of laboratory-reared specimens. These agree closely with the head widths of bugs collected from Doornhoek Cave and examined in 70% alcohol.

TABLE 1

Head widths of individuals of *S. antennatus*

| *Stage* | *No. used* | *Range* (mm) | *Mean* (mm) | *S.D.* (mm) |
|---|---|---|---|---|
| 1st instar . . . | 10 | 0,40–0,48 | 0,440 | 0,027 |
| 2nd instar . . . | 12 | 0,48–0,54 | 0,515 | 0,025 |
| 3rd instar . . . | 15 | 0,55–0,66 | 0,638 | 0,023 |
| 4th instar . . . | 15 | 0,68–0,78 | 0,742 | 0,018 |
| 5th instar . . . | 15 | 0,80–0,88 | 0,826 | 0,020 |
| Adult male . . . | 10 | 0,86–0,98 | 0,877 | 0,024 |
| Adult female . . | 10 | 0,84–0,99 | 0,891 | 0,029 |

TABLE 2

Duration of the immature stages and mortality of *S. antennatus*. Animals were maintained at 22 ± 1°C and 75% r.h. and fed on rats.

| | | *Duration of stage (days)* | | | *Mortality* |
|---|---|---|---|---|---|
| *Stage* | *No.* | *Min.* | *Max.* | *Mean* | (%) |
| Egg . . . . | 88 | 6 | 11 | 8,3 | 12,5 |
| 1st instar . . . | 45 | 8 | 12 | 10,1 | 15,5 |
| 2nd instar . . | 32 | 7 | 14 | 12,5 | 9,4 |
| 3rd instar . . . | 26 | 7 | 18 | 15,3 | 7,7 |
| 4th instar . . . | 39 | 11 | 21 | 16,4 | 5,1 |
| 5th instar . . . | 18 | 13 | 20 | 17,0 | 5,6 |
| Total . . . . | | 52 | 96 | 79,6 | |

The durations of the various developmental stadia are shown in Table 2. Eggs laid on strips of filter-paper during one 24-hour period were transferred to an incubator at 22°C where the relative humidity was controlled at 75% by means of concentrated salt solutions (Winston & Bates 1960). Enclosed first instar nymphs were collected daily. The duration of nymphal instars was measured from the time of hatching or moulting. Bugs showed a period of 24 to 48 hours after moulting when they did not engorge, and the time between successive blood meals was at least five days, although hosts were offered thrice weekly. No unfed nymph was observed to moult, but moulting took place one to three days after engorgement. Specimens which were damaged as a result of transfer or handling were omitted from Table 2. Such rapid development as shown in Table 2 may be uncommon in the bat-roost, depending upon the availability of hosts.

TABLE 3

Survival of unfed, recently moulted individuals of *S. antennatus* at 22 ± 1°C and 75% r.h.

| | | *Survival in days* | | | |
|---|---|---|---|---|---|
| *Stage* | *No.* | *Min.* | *Max.* | *Mean* | *S.D.* |
| 1st instar . . . | 35 | 4 | 19 | 11,2 | 2,6 |
| 2nd instar . . | 16 | 10 | 28 | 15,5 | 4,3 |
| 3rd instar . . . | 32 | 6 | 26 | 18,6 | 3,6 |
| 4th instar . . . | 14 | 11 | 39 | 24,3 | 5,1 |
| 5th instar . . . | 19 | 21 | 54 | 30,1 | 4,5 |
| Adult male . . | 30 | 18 | >63* | >38,6 | |
| Adult female . . | 21 | 21 | >63* | >47,4 | |

*Observations terminated on day 63 when 3 males and 5 females remained.

The effects of starvation are shown in Table 3. Engorged individuals of all immature developmental stages were placed in an incubator at 22°C and 75% r.h., and exuviae and dead individuals were removed three days later. These dead bugs were assumed to have died from causes other than starvation, and they are excluded from Table 3. After the bugs had moulted (about three days after engorgement), the colony was checked daily for 63 days and dead individuals were removed and sorted by instar. Recently hatched first-instar nymphs which were allowed to feed were maintained separately under the same conditions and checked daily for dead individuals.

Collections were made from Doornhoek Cave in May 1975 by brushing batbugs off the walls and ceiling into a beaker of alcohol. Of 2 733 specimens collected in this manner and assigned to an instar, 382 were first instar nymphs (14,0%); 287 were second instar (10,5%); 394 were third instar (14,4%); 549 were fourth instar (20,1%); 648 were fifth instar (23,7%); and 473 were adults (17,3%). If mortality is greater in earlier instars, an assumption which is not contradicted by the mortality data in Table 2, one would expect to find a preponderance of early instars. In the absence of such a trend, we suggest that the collecting technique was biased or that the batbug population was stressed, possibly by a lack of food which resulted in either reduced oviposition or lowered survivorship of earlier instars. This latter is also suggested by the relatively few engorged batbugs (< 15%) obtained in the same sample.

The sex ratio of batbugs in the shaft was 1,69: 1,00 (males to females; n = 460). The sex ratio in a laboratory-reared colony was 1,07: 1,00 (n = 139). Assymetry of the sex ratio of other cimicids has been reported by Usinger (1966) who indicated that excessive matings, which are traumatic, took their toll of females. No fatal matings were observed in *S. antennatus*, and the biased sex ratio in the field may be due to other factors such as differential predation of females. These are larger than males, especially when engorged, and may thus be more easily wounded by their hosts or taken by predators, although survival of once-fed females exceeded that of once-fed males in the laboratory (see Table 3).

## POPULATION DENSITY

A survey of the batbug population at Doornhoek was undertaken to indicate the effects of parasitism on the host population and the factors which might be limiting to the growth of the parasite population. On 14 May 1975, bugs were collected with the brushing technique described above from swathes running up the walls and across the ceiling, each 0,5 m wide, spaced every 10 m along the shaft, beginning at the innermost end (5% of the cave surface thus being examined). From the inner collection site to the outermost, the numbers of bugs collected were 468, 226, 587, 310, 539, 271, 363, and 0, totalling 2 764 (mean=345,5±189,56). The total population of batbugs was thus estimated as 55 000. The distribution of bugs in the cave was found to be uniform throughout, except in the area closest to the entrance. The outermost collection site was within two metres of the opening and well lit. This suggested an avoidance of more intense illumination, as was later confirmed in the laboratory. Bats retreat to the blind end of the shaft as one enters, but the pattern of guano on the floor indicates that the entire length of the shaft is utilized as a roost. The distribution of bugs also reflects this pattern of usage.

The bat population of Doornhoek Cave varies from about 150 to 900 individuals, fewer bats residing there during the winter months of June to the end of October (Wingate, in prep.). The approximate mean number of bugs per host in the shaft during May 1975 was 220, based on an estimate of 250 bats supporting 55 000 ectoparasites. Such a parasite-load could result in estimated average daily blood loss per host of 84 mg, if the blood meal size of *S. antennatus* is assumed to be the same as in *C. lectularius* (Titschack 1930, in Usinger 1966) and each batbug feeds once per 10 days.

The frequent grooming motions and irritability of apparently healthy bats may serve to minimize the number of batbugs feeding on them because such bats were seen to harbour few bugs. In contrast, an abandoned and enfeebled *Myotis tricolor* infant was seen by L. R. W. to have been covered by a large number of batbugs. It died the following day, and it is suggested that the batbugs hastened, if not caused, its demise. Successful host reproduction and constant occupancy of the shaft, as well as the presence of competing ectoparasites (Streblidae, Nycteribiidae and Polyctenidae), indicate that the batbugs are not significantly debilitating to the bats at Doornhoek.

The batbug population in turn is thought to support several predators. Fourteen unidentified reduviid nymphs were found. These were covered with fibrous debris or duff in the manner described by Usinger (1966) for the 'masked bedbug hunter', *Reduvius personatus*. When cleaned of debris, these assassin bugs had a reddish colour to the abdomen, derived most likely from the bat-blood consumed by their batbug prey. In the laboratory these nymphs were seen to kill and feed on numerous batbugs. The shaft also houses a large population of pseudoscorpions which could be seen among the batbugs on the walls and ceiling, but these, like the numerous spiders and the infrequently found tailless whip scorpions (Amblypygi: Tarantulidae: *Damon variegatus*), were not observed to feed on batbugs. In an attempt to determine the possible extent of predation by the insectivorous host bats themselves, batbugs were hand-fed to adult *Rhinolophus clivosus*. These would accept meal-worms but not batbugs, which they bit and spat out. A laboratory rat which was used for feeding the batbug colony in the laboratory, however, ate several dozens of bugs before it was restrained.

## BEHAVIOUR

*S. antennatus*, like most other cimicids which have been observed (see Usinger 1966), is a nidicolous parasite (nest-dwelling in the terminology of Audy 1958), living in the bat-roost where it finds hosts and shelter and not usually remaining on a host when it leaves the roost. This is borne out by the absence of batbugs on bats netted outside of the shaft and by the observation that the bug parasitizes several species of bats in the cave, even those of different families. The batbug has no specialized organs of attachment, such as those of polyctenids, with which it might gain purchase on its host. It is easily removed from a bat, in contrast to the resistance one encounters when removing a batfly (Streblidae or Nycteribiidae) or polyctenid from its host. The relatively long legs of this batbug may, rather, be adapted for walking over the rough surfaces of the substrate. When disturbed by attempts to catch them with forceps, batbugs drop to the floor. This response can also be evoked by directing a stream of air at them, suggesting a mechanism whereby the insect would, in the first instance, avoid the grooming motions of its host and, in the second, prevent itself from being carried out of the bat-roost. In contrast, Kemper (1936, in Usinger 1966) reported that drafts cause the bedbug to cling to the substrate.

Batbugs could be seen walking up the walls of the cave, suggesting a geo-negative orientation. This was also observed in the laboratory where batbugs would climb vertically up a rough piece of wood for distances of 2 m in the dark. (To contain the colonies, 1 litre glass beakers were used whose sides were apparently too smooth for the bugs to negotiate.)

Batbugs may also remain in the bat-roost as a result of their photo-negative reactions, both tactic and kinetic. In a circular arena 14 cm in diameter, half of which was illuminated with diffuse light and half darkened, no batbugs remained on the lit side after 24 hours in 10 trials with 10 batbugs each. Responses to directed, more intense light were pronounced: 47 of 50 adult batbugs turned and walked away from the light source (a microscope lamp) and 3 remained stationary.

The clustering of batbugs in cracks in Doornhoek Cave suggested a thigmo-positive orientation. In a uniformly lit arena, bugs congregated under a curved watchglass, obtaining contact of the dorsal and ventral surfaces of their bodies with the watchglass and the arena floor without gaining reduced light intensity. Similarly, bugs would come to rest over scratches and cracks in the glass floor of another arena, and a rougher substrate such as rock or wood was significantly preferred over glass or smooth plastic. In a uniformly smooth circular arena whose walls slope away from the floor adult and immature bugs would cluster together. If the bodies of dead bugs were placed in such an arena, aggregations of bugs would form around them, although these corpses were not significantly preferred over small pieces of wood or stone in attracting aggregating individuals, and they are most likely perceived as irregularities in the arena. Oviposition-site selection, likewise, indicates a tactile choice of substrate. Of thousands of eggs laid in laboratory colonies, only a few were found to have been deposited on glass. Filter-paper and, to a greater extent, wood were the preferred substrates.

The facilitation of both aggregation and dispersal in bedbugs is promoted through assembly and alarm pheromones (see Levinson *et al.* 1971, 1974). The bioassays of Levinson *et al.* (1971) were repeated for *S. antennatus*, but no clear evidence of pheromonal communication was obtained. Batbug aggregations were not dispersed by exposure to hexen-l-al, a component of bedbug alarm pheromone, whereas bedbug clusters were rapidly broken up by the vapours. Bedbugs would even stop feeding and exhibit escape reactions when stimulated by the hexen-l-al. Antennectomized adult batbugs remain capable of aggregating, suggesting that this reaction may be tactile rather than chemosensory. Although these preliminary observations do not suggest the presence of pheromones in *S. antennatus*, such compounds may be present since batbug colonies have a distinctive odour whose function is unknown.

Batbugs in the shaft found hosts in their immediate vicinity, and it is doubtful that they possess long-distance preception of host-emitted stimuli. In the laboratory starved bugs could be seen distributed throughout a dimly lit arena, whereas engorged bugs, obvious by the red colour of their abdomens, were normally aggregated (12 trials with 10 fed and 10 unfed adult bugs each, tested with Chi-square 2X2 contingency table, $P < 0{,}01$). Increased locomotion in unfed bugs, then, might result in the finding of a host by chance. Adult bugs were significantly attracted from short distances ($< 5$ cm only) to an aluminium foil-covered test-tube containing water at 35°C, compared to a tube at ambient temperature (20°C) when both were presented simultaneously (five trials lasting 5 minutes each with 25 adult bugs each, tested with Chi-square test, $P < 0{,}05$). This attraction was abolished by recent engorgement (two trials with 10 engorged and 10 unfed adult bugs each, tested with Chi-square 2X2 contingency table, $P < 0{,}05$) and by antennectomy (four trials with 10 normal unfed and 10 antennectomized unfed adults each, tested with Chi-square 2X2 contingency table, $P < 0{,}05$). Similarly, unfed batbugs are not attracted to a dead rat unless it is either recently dead or warmed above ambient temperature. In the bat-roost the body temperatures of bats were normally above that of their surroundings. Very few torpid bats were found during the study. It would thus seem likely that temperatures are a clue utilized by batbugs in recognizing, if not finding, hosts. Since active bats have a higher body temperature than do ones which are resting, one could suggest that bats which have recently flown into the bat-roost might be more attractive to the batbugs.

In a darkened rectangular arena (10 by 20 cm) which offered a choice of equal areas of differing relative humidity, maintained with saturated salt solutions (Winston & Bates 1960), batbugs at 20°C were indifferent to humidities between 12,5 and

92% r.h. and repelled by humidities outside of this range. Bugs were tested singly since groups of bugs tended to come to rest more rapidly than did single individuals, suggesting that a stimulus for aggregation may compete with relative humidity. Even unfed adults were not attracted to 98% r.h. when offered an alternative of 76% (16 adults tested singly, tested with Chi-square, $P < 0{,}01$). This indicates that, although perception of water-vapour exists, batbugs do not appear to utilize relative humidity as a stimulus in finding hosts whose exhaled breath would presumably be close to saturation.

Host odour in the absence of warmth was also unsuccessful in eliciting oriented responses from batbugs. Filter-paper discs 25 mm in diameter which had previously been placed in contact with a laboratory rat for 8 hours were not preferred over controls (three trials of 20 unfed adults each, tested with Chi-square, $P > 0{,}3$), and filter-paper which was taped to W. L. O.'s arm before being presented along with a control was slightly repellent (three trials of 20 unfed adults each, tested with Chi-square, $P < 0{,}1$). Thus no role for olfaction in host-finding was found, although its importance in host-recognition was not investigated.

That batbugs, like bedbugs, are excited by carbon dioxide was seen when carbon dioxide was used as an anaesthetic. When exposed to carbon dioxide, bedbugs ran and the characteristic sweet smell of alarm pheromone was given off. Batbugs, also, began rapid movements but no strong odour was detectable. Low concentrations of carbon dioxide (approximately 5% obtained by mixing $CO_2$ and air in a plastic bag) caused increased locomotion in unfed adults. Thirty unfed adults were tested on two successive days in an arena with a 1 cm grid. The number of grid lines crossed per individual bug in five minutes was counted, and results tested against the null hypothesis of 'no change' with Chi-square. The frequency and average distance of walking was significantly increased upon exposure to the carbon dioxide–air mixture ($P < 0{,}05$ for both). Directed responses towards areas of higher carbon dioxide concentration were not tested, but the observed responses make it possible that carbon dioxide concentration aids host-finding by stimulating locomotion, increasing the chances of a batbug coming into contact with a host.

## CONCLUSIONS

The population of *S. antennatus* in Doornhoek Cave, although estimated to be in excess of 50 000 individuals, does not appear to strain the resources of its hosts. A limiting factor for growth of the batbug population may be host-availability, as indicated by the frequencies with which early instar nymphs were collected, even though hosts are present in the roost throughout the year. The bugs probably breed throughout the year since neither lack of hosts nor low temperatures would seem to preclude reproductive activity.

Developmental rates obtained in the laboratory for the five nymphal instars, utilizing bugs fed on rats as soon as moulting took place, are no doubt greater than those which would prevail in the bat-roosts where access to a host may be limiting and full engorgement not always possible. Nevertheless, such rapid development could permit a large population build-up if a surplus of hosts should become available. In times of limiting food availability, however, it is assumed that adults and fifth instar nymphs would survive while earlier instar nymphs would die. This pattern was seen from collections made in May, when host populations were not at their peak.

People bitten by batbugs suffered only slight discomfort. While these bugs may be brought into houses by bats, there is probably little danger to the human occupants. The reluctance of these batbugs to feed on human beings makes it unlikely that they would continue to infest a human dwelling in the absence of bats.

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